

Research Article

A population dynamics approach to understand the invasiveness of the seaweed *Rugulopteryx okamurae* (Ochrophyta, Dictyotales)

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Abstract

The success of invasive species can be measured by invasiveness, which depicts intrinsic characteristics that enable them to thrive in new environments. In invasive seaweeds, for example, the persistence of multiple overlapping cohorts throughout the year plays a key role in increasing plant cover and exerting unrelenting pressure on invaded areas. The marine brown macroalgae *Rugulopteryx okamurae* has recently established abundant populations in the Mediterranean Sea and Atlantic Ocean, negatively affecting both biodiversity and socioeconomic factors by unprecedentedly aggressive invasive behaviour. The objective of the study is to understand the invasiveness of *R. okamurae* through its population dynamics. For this, a year-round study was conducted in a protected habitat of *Posidonia oceanica* in southern Spain, revealing that *R. okamurae* uses alternating mechanisms for population maintenance. It achieves high density of young individuals in late summer and autumn, peaking at 3285 individuals per square metre. In spring and early summer, the population shifts towards fewer – but larger – individuals, with densities dropping to 888 individuals per square metre and biomass reaching a peak of 170 g dry weight (DW) per square metre. Six overlapping cohorts were identified by Gaussian curves. They persisted throughout the year, but they were not related to environmental factors, which indicates adaptive physiological mechanisms that sustain dense monospecific populations. Additionally, the association between cohorts and different morphotypes suggests that *R. okamurae* phenotypic plasticity enables its persistence in introduced areas. These findings provide valuable insights into the biological traits underpinning its invasiveness in *P. oceanica* meadows, revealing temporal windows of invasiveness driven by different mechanisms. This knowledge is crucial for developing effective conservation and management strategies aimed at mitigating the impact of this invasive species.

Key words: Demography, density, generation, macroalga, *Posidonia oceanica*, recruitment



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Introduction

Invasion success refers to an invasive species' ability to progress through all stages of invasion, from introduction to dispersion, by overcoming ecological barriers and progressing through successive stages of establishment and expansion in a new environment (Gioria et al. 2023). Studies aiming to identify and understand the factors that contribute to the success of invasive species have led to the development of various invasive hypotheses (Lowry et al. 2013). Currently, there are

more than thirty invasion hypotheses that try to explain the relationship between invasive species, invaded communities and their interactions (Enders et al. 2018). According to Gioria et al. (2023), invasion hypotheses can be grouped into three major categories, namely: (1) propagule pressure, which involves the introduction efforts by invasive species in a new area and is defined as the number and frequency of propagule release (Lockwood et al. 2005; Colautti et al. 2006), (2) invasibility, referring to the characteristics of the receiving ecosystem and its susceptibility to being invaded (Catford et al. 2012; Colautti et al. 2014) and (3) invasiveness, referring to intrinsic characteristics of the species, including functional traits that determine its invasive potential (Pyšek et al. 2014; Jehangir et al. 2024). In this context, identifying the traits that serve as good predictors of invasiveness involves several factors, including physical performance, growth rate, size, biomass allocation, physiology and phenotypic plasticity (Richardson and Pyšek 2006). The latter expands the range of responses to biological and abiotic factors encountered in introduced areas, allowing the species to adapt quickly to the new environment and facilitating their establishment and expansion (Richards et al. 2006). This trait has been used to evaluate invasiveness by comparing population abundances and survival rates with native populations (Ebeling et al. 2008; Colautti et al. 2014). Collecting censuses across all major life stages of invasive species and employing demographic models are essential tools for gaining deeper insights into the population dynamics of invasive species (Williams et al. 2010; Colautti et al. 2014).

The study of seaweeds' invasiveness has predominantly focused on a limited number of species (Dalla Vecchia et al. 2020). The common traits that contribute to their invasiveness are morphology, physiologic plasticity, productivity and reproduction. These are the most studied characteristics (Mabey et al. 2023). Invasive seaweeds often show rapid growth rates and early maturation of reproductive structures, which allows them to quickly establish and spread in new environments (South et al. 2017; Zanolla et al. 2017). Other traits, including multiple overlapping cohorts maintained by both older individuals and new recruits, were described for *Undaria pinnatifida* (Harvey) Suringar (Schiel and Thompson 2012) and *Asparagopsis taxiformis* (Delile) Trevisan (Zanolla et al. 2019). This ability to persist year-round in introduced areas has been attributed to their morphological and physiological plasticity (Campbell 1999; Zanolla et al. 2015).

Rugulopteryx okamurae (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotaceae, Phaeophyceae), a flattened brown seaweed with dichotomous branching (Hwang et al. 2009), is native to the western Pacific Ocean (Verlaque et al. 2009). Starting as an unprecedented cryptic invasion in the western Mediterranean in 2015, it now forms abundant populations in Spain, including the Canary Islands and the Chafarinas Archipelago (Altamirano et al. 2016; REDEXOS 2022); France (Ruitton et al. 2021); Italy (Bellissimo et al. 2024); Morocco (El Aamri et al. 2018); and Portugal, including the Azores and Madeira (Faria et al. 2021; Bernal-Ibáñez et al. 2022; Liulea et al. 2023). Currently, *R. okamurae* continues its expansion both in the Mediterranean Sea and the Atlantic Ocean, being most recently recorded in northern Spain, which indicates a worrying upward trend in its spread (Díaz-Tapia et al. 2024). Predictive models suggest that the European and north African coasts are highly favourable habitats for this species, so it is likely that its expansion will continue in the coming years (Muñoz et al. 2019). Like other Dictyotaceae species, *R. okamurae* exhibits a digenetic isomorphic life cycle, alternating haploid gametophytes with diploid sporophytes. At a morphological

level, it presents up to three different morphotypes throughout the year in both native and introduced areas (Sun et al. 2006; Salido and Altamirano 2020). The species can reproduce by propagules, asexually by mitotic monospores and sexually by gametes and meiotic tetraspores, but gametangia have only recently been observed in northern Spain (Díaz-Tapia et al. 2024).

Rugulopteryx okamurae can settle on both horizontal and vertical rocky surfaces within a bathymetric range from eulittoral zones to depths of more than 50 m (García-Gómez et al. 2018; Altamirano et al. 2019). In southern Spain, *R. okamurae* has seriously impacted native flora, including the seagrass *Posidonia oceanica* (Linnaeus) Delille (García-Gómez et al. 2018; Junta de Andalucía 2019). *Posidonia oceanica* is a native seagrass listed in the Spanish List of Wild Species under the Special Protection Regime (*Listado Español de Especies Silvestres en Régimen de Protección Especial y Catálogo Español de Especies Amenazadas*) (Real Decreto 139/2011). It is also considered to form a priority habitat by the Habitats Directive (Council Directive 92/43/EEC). Similar impacts on native flora have been observed in the Azores Islands (Faria et al. 2022), where *R. okamurae* is replacing dominant species and altering the structure of shallow-water benthic communities. The fast and abundant proliferation of *R. okamurae* biomass not only produces high environmental impacts, but also socioeconomic ones (Altamirano et al. 2016; MITECO 2022). In particular, the fishing industry has been suffering economic losses estimated in millions of euros because of a decrease in fish stocks (MITECO 2022). Moreover, the extensive efforts to remove castaway biomass accumulated from beaches in tourist areas is also affecting local administrations (MITECO 2022). All these impacts have led to its inclusion in the List of Invasive Alien Species of Union Concern, being the first seaweed to be added (Commission Implementing Regulation (EU) 2022/1203 of 12 July 2022 amending Implementing Regulation (EU) 2016/1141). However, despite numerous studies about the species' potential biotechnological uses (e.g. Romero-Vargas et al. (2024)), only few studies focused on its basic biology, which is key to our understanding of the risks associated with its invasion and to lay the groundwork for implementing effective conservation and management strategies for affected marine ecosystems.

In this context, the objective of the present study is to understand the invasiveness of *R. okamurae* by analysing its population dynamics on an invaded *P. oceanica* meadow in southern Spain and exploring the relationship of several demographic descriptors with abiotic environmental factors throughout the year.

Methods

Study area and sampling procedure

The study was conducted on a population of *R. okamurae* established on a *P. oceanica* meadow located in front of Cambriles Cliff, Granada, Spain (36°44.0033'N, 3°20.6767'W), at a depth of 10 metres (Fig. 1). This *P. oceanica* meadow is 48 hectares in extent, ranging from 7 metres to 13 metres in depth (Portal Ambiental de Andalucía 2024).

Sampling for the study was carried out by scuba every two months from July 2021 to July 2022. Due to the protected status of the *P. oceanica* habitat (Real Decreto 139/2011) and the status of the invasive species *R. okamurae*, appropriate permits were obtained from the relevant authorities. Prior to the study, the minimal sam-

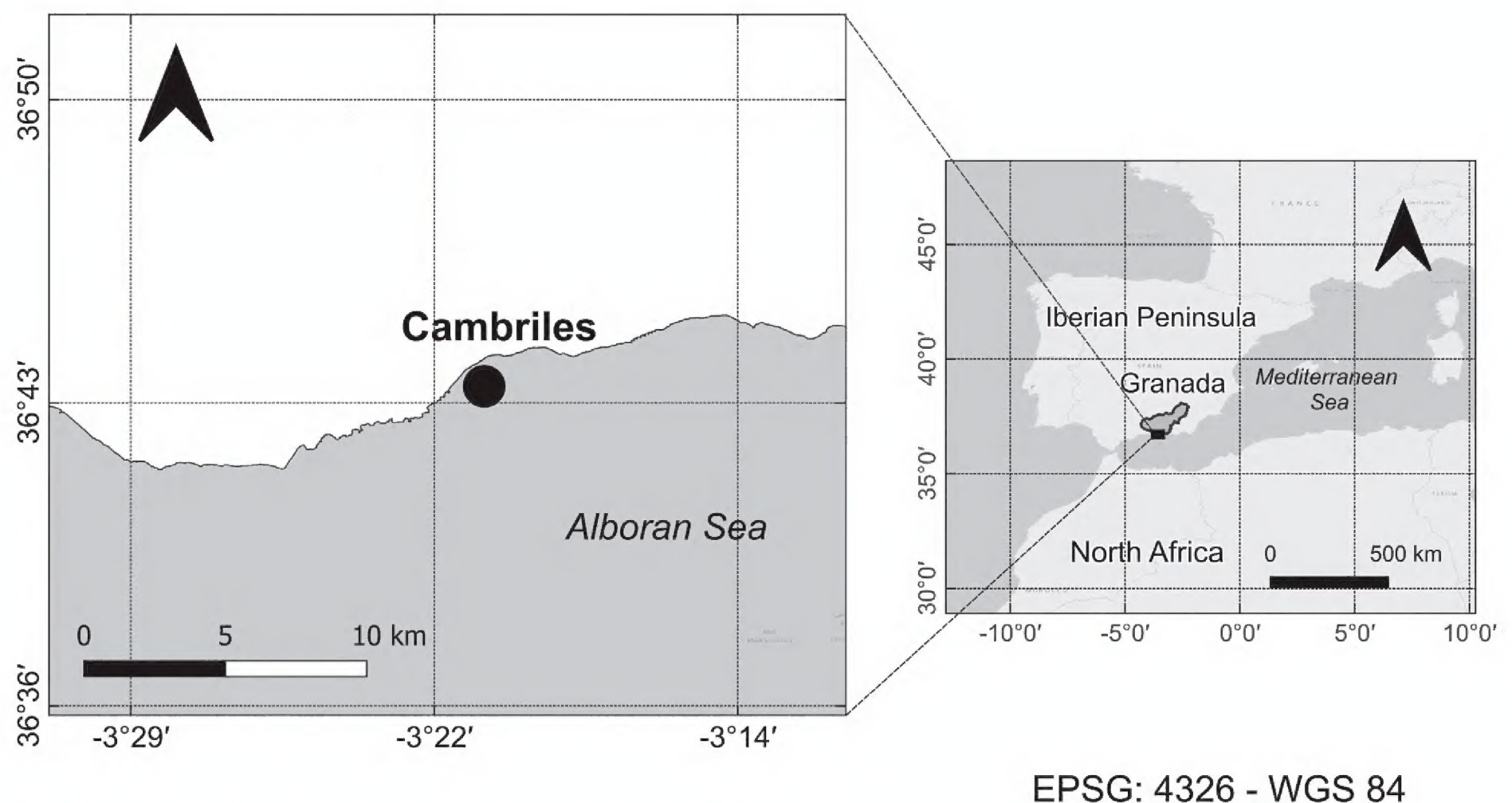


Figure 1. Sampling site of *R. okamurae* in Cambriles cliff, Granada (Spain).

pling area of *R. okamurae* was estimated following Cain and Castro (1959). All algal material in three one-metre by one-metre quadrats, each subdivided into 20 cm × 20 cm squares and spaced five metres apart, was carefully scraped and bagged separately in plastic bags. Samples were transported to the laboratory for weighing and for estimating the minimal sampling area through iterative measurements of contiguous squares. The process involved analysing the abundance data to estimate the smallest square size that showed no statistical differences in abundance between contiguous squares and through the estimation of the aggregation index, based on the ratio of variance to mean biomass, as described by Blackmann (1942). The minimum sampling area was 30 cm × 30 cm. Thus, within three areas with a homogeneous biomass density of *R. okamurae*, four replicates of the minimal area were taken and collected at the same depth, separated by 5 m between sampling areas. All algal material was thoroughly removed avoiding damaging *P. oceanica* plants and placed in plastic bags, preventing accidental dispersal of *R. okamurae*. Subsequently, the samples were transported to the laboratory under cold and dark conditions for further analysis.

Population dynamics

All individuals within each sample were measured from the base of the thallus to the most distal dichotomy and categorised into eight different size classes in two-centimetre increments, except the first class (four centimetres), which corresponds to young individuals or recruits. The abundance of *R. okamurae* was estimated as the number of individuals and their dry weight (DW) biomass per square metre for each sampling event. Dry weight biomass was quantified after drying at 60 °C for 48 hours in an oven. Distribution frequency of size classes plots was constructed using the percentage of individuals in each size class against the total number of individuals in each replicate and the mean values calculated. Cohorts, defined as individuals sharing a particular event during their lifespan (Crisp 1971), were

identified by tracking the displacement of Gaussian curves in the frequency versus time histograms, based on distributions of size classes along the year (Aranda et al. 1984; Zanolli et al. 2019). If more than one cohort overlapped within a given sampling time, a separation was achieved through a numerical fit using Gaussian curves (Petersen 1912; Zanolli et al. 2019). Each cohort was represented using all replicates by a Gaussian curve characterised by its mean and standard deviation (SD) through the Distr. Norm function. The adjustment of these parameters was performed using the SOLVER application (Excel, Windows Office 365). Finally, a statistical comparison of each mean and SD from the curves was carried out using a t-test statistical analysis. If no statistical differences were found, we assumed the existence of a single cohort. The model's significance was validated through R^2 .

Environmental factors

Daily data on average temperature, maximum and minimum temperature and salinity from a buoy situated near the study area were obtained from Puertos del Estado website (Ministerio de Transportes y Agenda Urbana), (SIMAR 2044080; 36.67°N, 3.5°E). The photoperiod was provided by the Observatorio Astronómico Nacional website, located in Granada (Instituto Geográfico Nacional, Ministerio de Fomento). In addition, three seawater samples were collected on each sampling date at the same depth as the *R. okamurae* population and analysed using an automated nutrient analyser QuAatro AQ2 AACE (Seal Analytical Ltd. Fareham, UK) for ammonium (Slawyk and MacIsaac 1972), nitrate and nitrite (Shinn 1941; Wood et al. 1967) and phosphate (Murphy and Riley 1962) following standard procedures.

Statistical analysis

Each biological variable was analysed using a one-way model ANOVA ($P < 0.05$), with time as a fixed factor. Homoscedasticity and normality were tested prior to the ANOVA by Levene's and Saphiro-Wilks test, respectively. When significant differences were found for a given biological variable, the Student-Newman-Keuls test (SNK) was applied for post hoc comparisons. Statistical analyses of ANOVA were carried out by SigmaPlot 11.0 software (Systat Software Inc., Chicago, IL, USA). To assess the relationship between environmental factors and biological variables, a principal component analysis (PCA) was conducted. An environmental space was constructed with axes derived from PCA using environmental factors and plotted in InfoStat version 2008 (Di Rienzo et al. 2008). Subsequently, Pearson correlations were used to investigate the relationship between biotic variables (density of individuals and biomass of *R. okamurae*) and the two principal axes derived from PCA (PC 1 and PC 2). These environmental axes produced in PCA were computed with the software PAST (Hammer et al. 2001).

Results

Population dynamics

Rugulopteryx okamurae was present throughout the whole year, displaying significant differences (DF: 6, F-value = 6.5, $P = 0.002$, Appendix 1) in density of individuals for different months (Fig. 2A). The highest values were recorded in September and No-

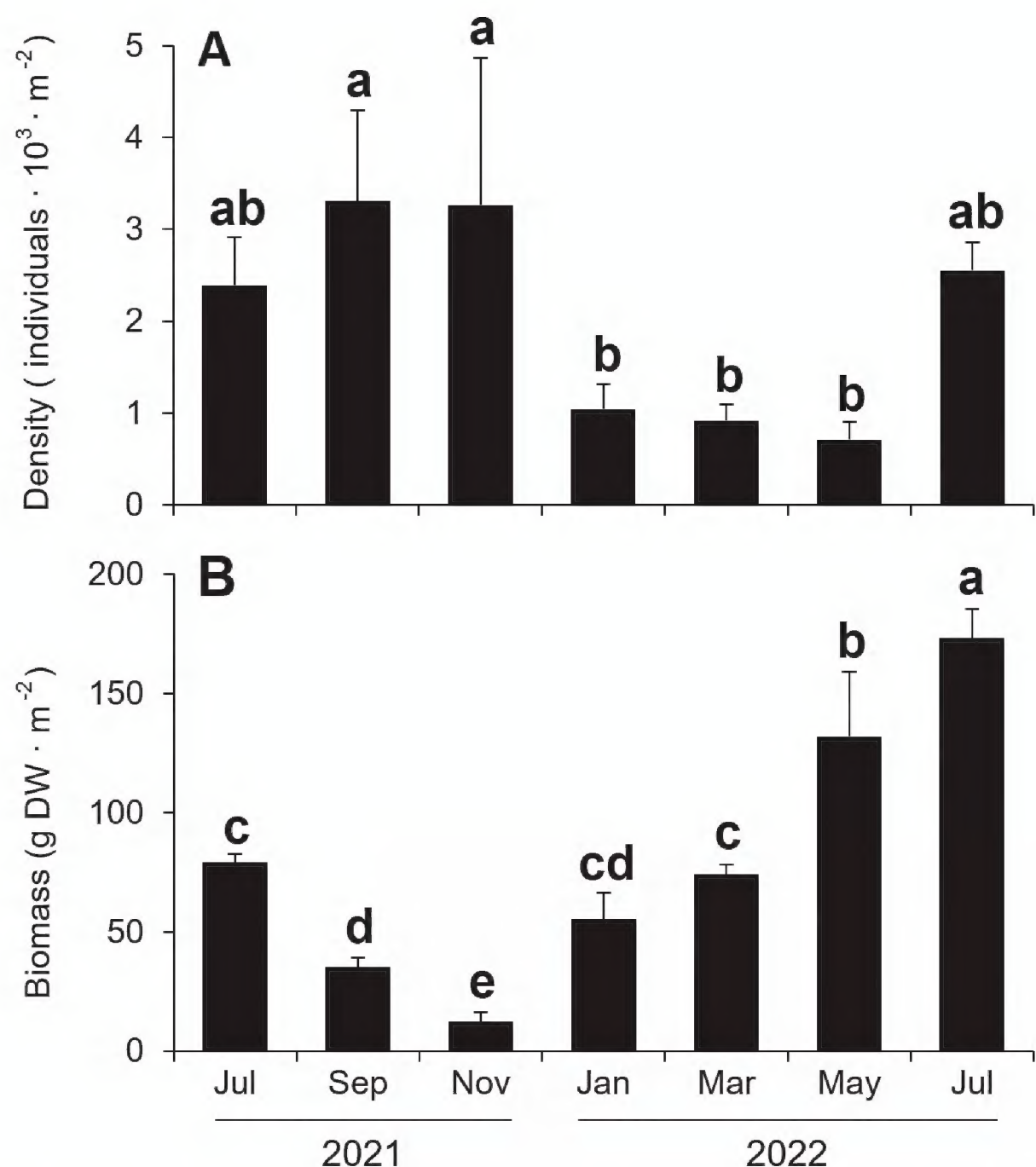


Figure 2. Density of *R. okamurae* throughout the study period (July 2021–July 2022) referred as **A** individuals (10^3 individuals per square metre) and **B** biomass (g DW per square metre). Data are expressed as mean $\pm$ SD ($n = 3$). Different letters denote significant differences among months following ANOVA results ($P < 0.05$).

vember, with an average value of 3285 individuals per square metre, whereas the lowest values were observed in January, March and May, with a decrease of more than one-third (888 individuals per square metre) (Fig. 2A). There were also significant monthly differences in biomass (Fig. 2B, DF: 6, F-value = 60.6, $P < 0.001$, Appendix 1). These values increased from November to July 2022, when they were 14 times higher.

The distribution of size classes varied throughout the year, reaching 18 cm in May and July 2022, representing less than 3% of the total individuals in those months. In contrast, in November, individuals did not exceed six centimetres (Figs 3, 4). Over 70% of the total population belonged to the size class of 0–4 cm in September and November (Figs 3, 4). However, there was an 85% reduction in the density of the smallest size class from November to January and it continued to decrease until May, when the lowest numbers were recorded (Figs 3, 4).

Cohorts

The frequency distribution of thallus size classes followed a normal distribution, revealing the presence of six cohorts (named using Roman numerals I to VI) with different longevity and temporal distribution (Fig. 4). The longest cohort started in

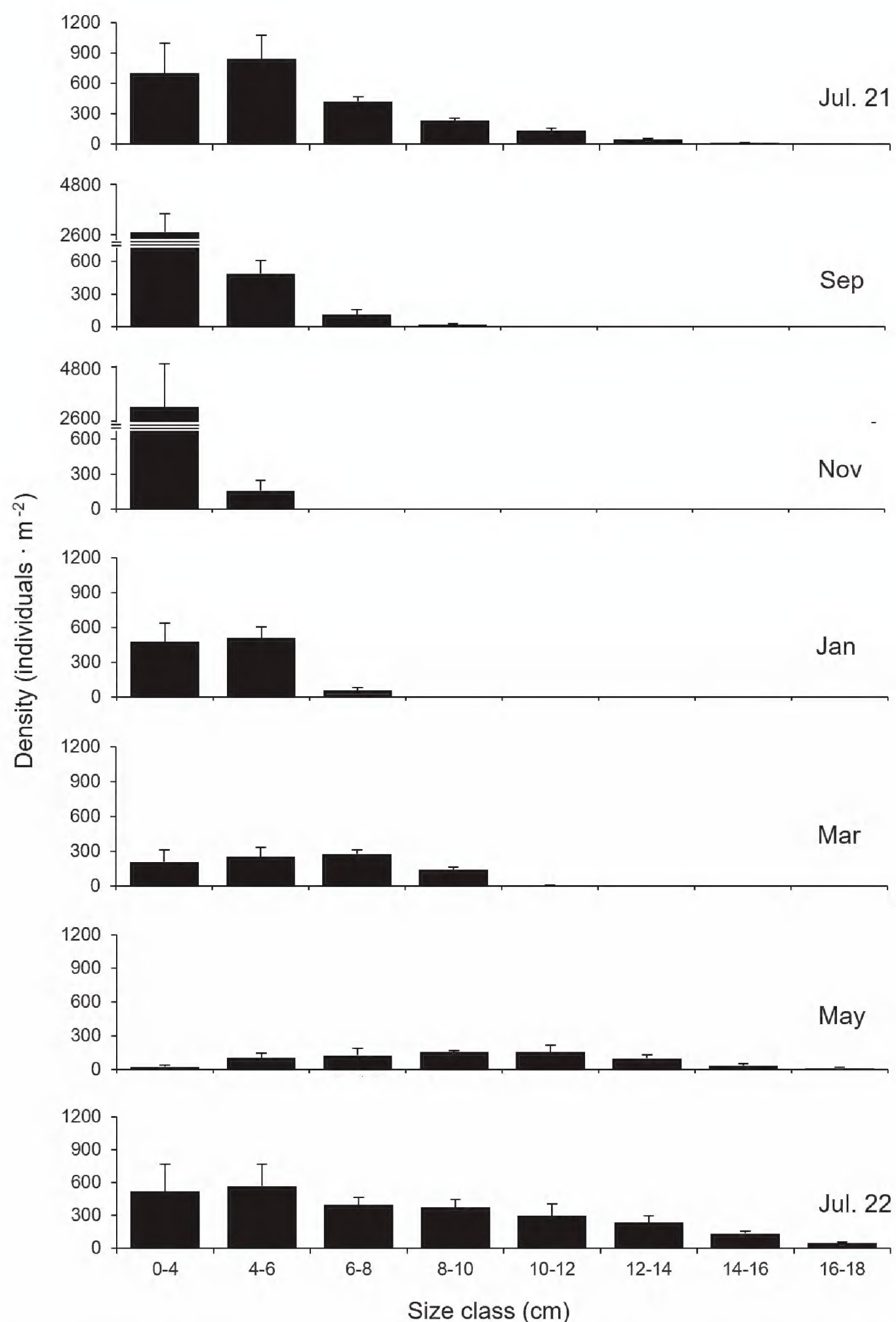


Figure 3. Density (individuals per square metre) of each size class throughout the study period (July 2021 to July 2022). Data are expressed as mean $\pm$ SD (n = 3).

November and persisted until May (cohort IV), while cohorts I, III, V and VI had a lifespan of one month each (Fig. 4). Cohort II was present in July and September 2021. The composition of these cohorts also showed variations (Fig. 4). Cohort III was composed solely of young individuals, whereas cohorts IV and VI included individuals from different size classes, including individuals up to 18 cm (Fig. 4). However, it took six months for plants in cohort IV to achieve the largest size class, but only two months for those in cohort VI (Fig. 4). Additionally, overlapping cohorts were observed in July 2021 (cohorts I–II), September (II–III) and May (V–VI) (Fig. 4).

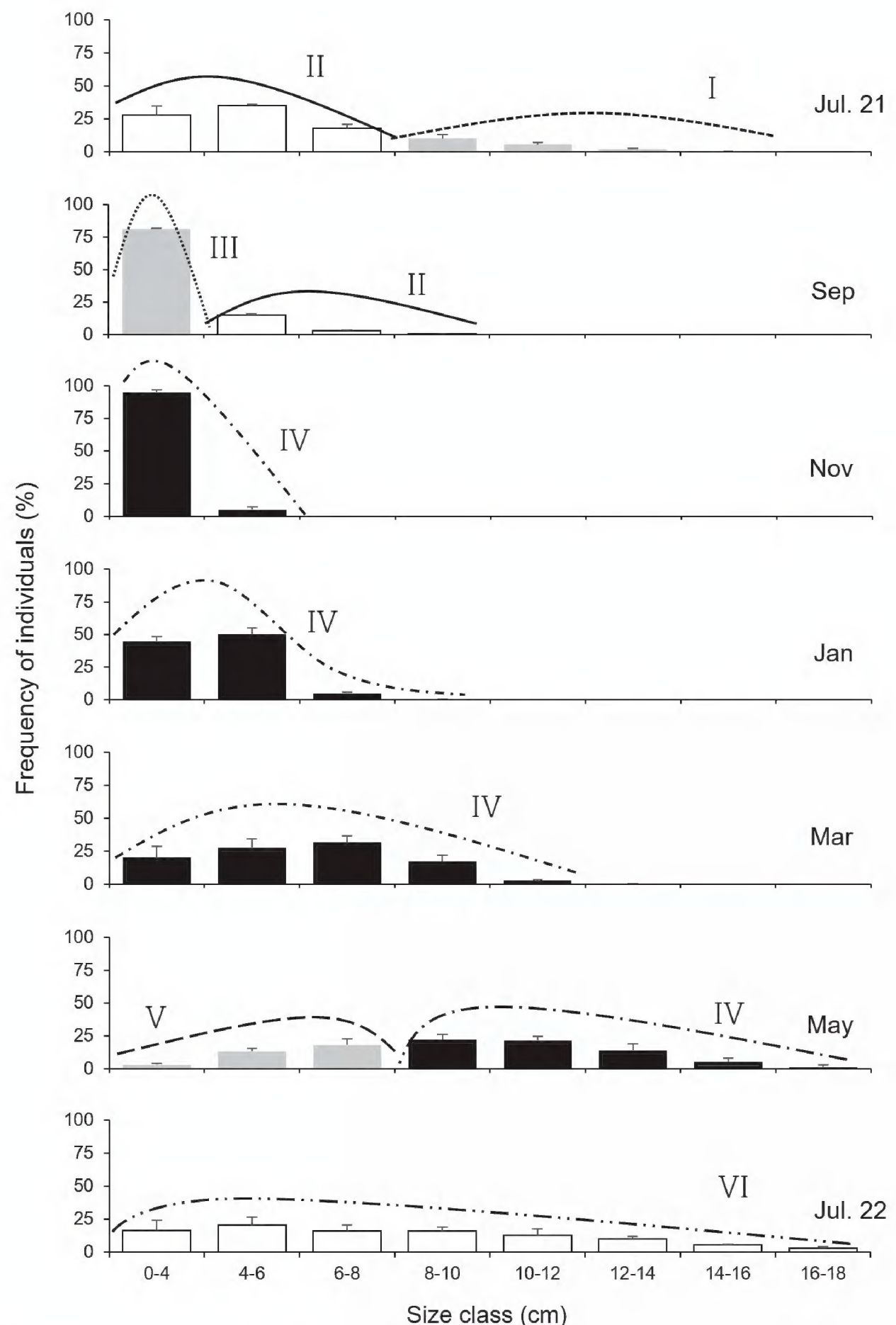


Figure 4. Frequency of individuals of each size class (%) related to the total of individuals of *R. okamurae* in each sampling event. Discontinuous lines indicate the six cohorts (labelled I to VI) found throughout the study (July 2021–July 2022). Values are expressed as means $\pm$ SD ($n = 3$).

Environmental factors

Average temperature ranged from 15 °C to 23 °C, with the maximum temperature registered in August 2021 (25.1 °C) and the minimum (14.8 °C) in January (Fig. 5A). Low variability (> 1 °C) was registered in the winter months but, in summer 2021, it reached a difference of 8 °C (Fig. 5A). The photoperiod varied within a range of 10 to 14 hours (Fig. 5B). Salinity remained relatively stable during the study period, ranging from 36.8 to 37.3 (Fig. 5B).

Nitrate concentration during the study period ranged from < 0.2 μM (the detection limit of the analytical method) to 1.4 μM (Fig. 6). Ammonium concentration did not display significant seasonal variations, oscillating between 0.5 and 1.6 μM (Fig. 6). Concentrations of nitrite and phosphate were too low to be detected (< 0.2 μM).

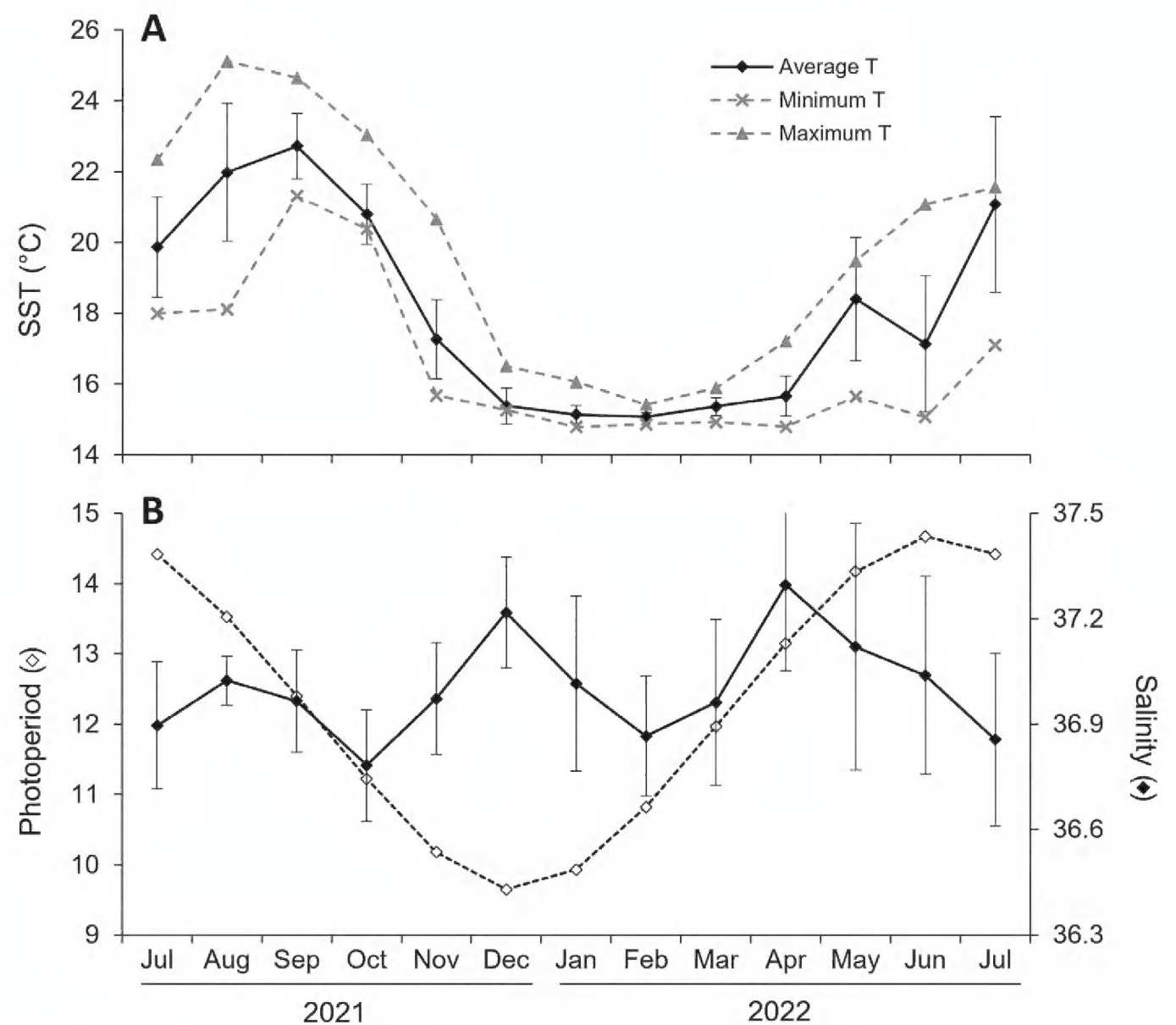


Figure 5. Environmental factors during the study period (July 2021–July 2022) in the study area (buoy SIMAR 2044080) **A** average data of mean, maximum and minimum temperature **B** monthly average photoperiod (dotted line) and salinity levels (solid line). Data expressed as mean $\pm$ SD of daily data.

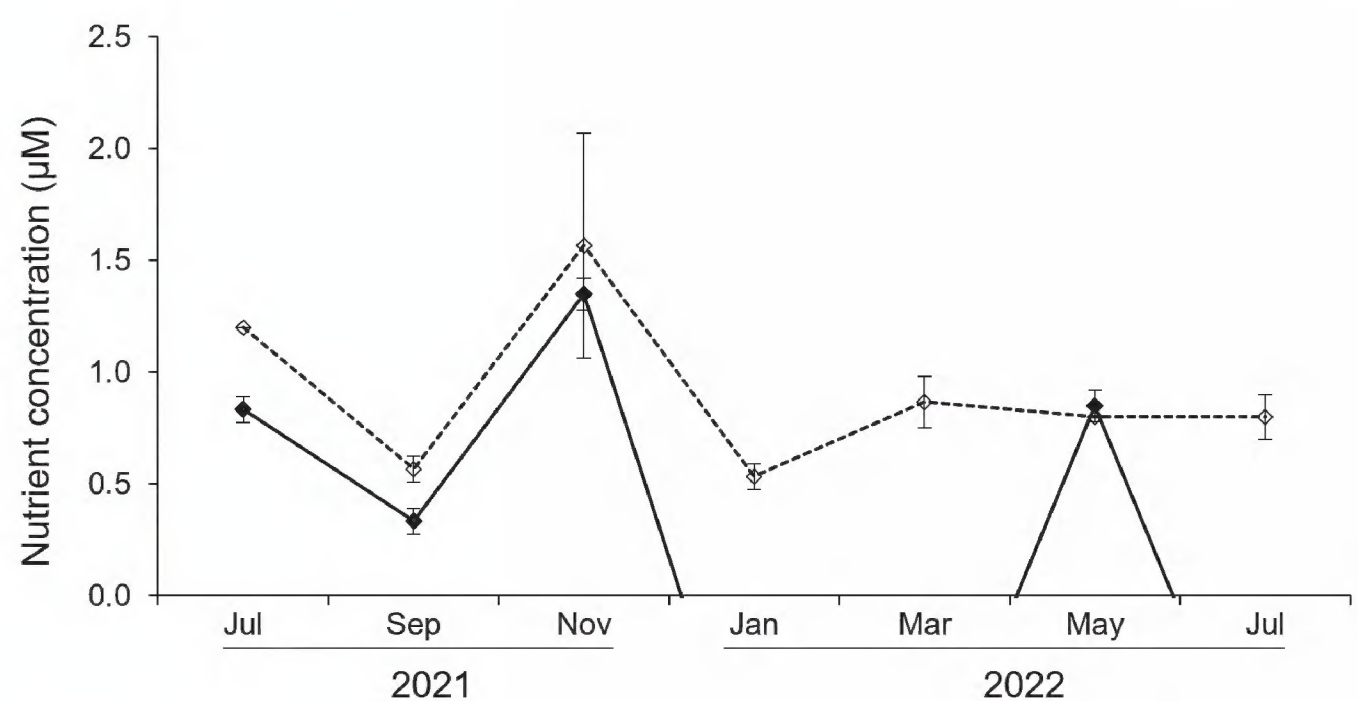


Figure 6. Nitrate (solid line) and ammonium (dotted line) concentration during the study period (July 2021–July 2022) in the study area. Data expressed as mean $\pm$ SD ($n = 3$).

Principal component analysis (PCA) of environmental factors indicated that specific abiotic factors contributed differently along the two main axes (PC 1 and PC 2), explaining 79.8% of the total variance (Fig. 7, Appendix 2). Temperature, photoperiod and salinity contributed mainly for the PC 1, while nitrate and ammonium concentrations were the primary factors contributing for the PC 2 (Fig. 7). Pearson analysis between biological variables (density of individuals and biomass) and the two principal components derived from the PCA showed no significant correlations (P values > 0.05 , Appendix 3).

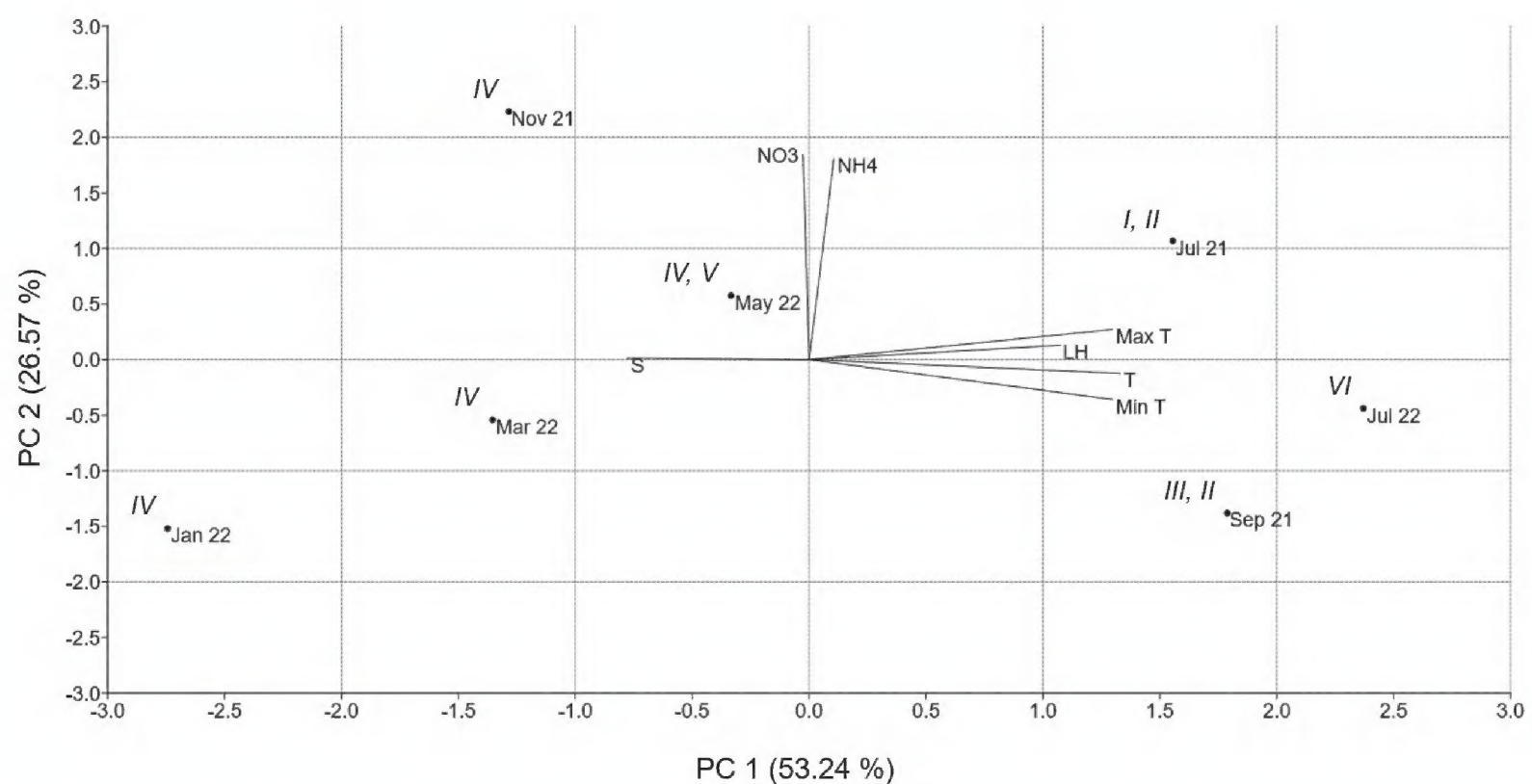


Figure 7. Environmental space derived from PCA constructed by environmental factors measured in the study area. Cohorts were labelled as I to VI. T, average temperature; Max T, maximum average temperature; Min T, minimum average temperature; S, salinity; LH, Photo-period; NO₃⁻, concentration of nitrate; NH₄⁺, concentration of ammonium; PC, principal component.

Discussion

Population dynamics of *R. okamurae* on a *P. oceanica* meadow during the year explains its invasive behaviour, characterised by the constant presence of a high density of individuals. This is achieved through its ability to continuously produce recruits and the presence of year-round short-lived overlapping cohorts that are not affected by the environmental parameters of the area.

The seaweeds' continuous presence is a characteristic of invasiveness shared amongst invasive seaweed species in invaded areas. Examples include the red seaweeds *Womersleyella setacea* (Hollenberg) R.E. Norris (Cebrian and Rodríguez-Prieto 2012), *Asparagopsis armata* Harvey (Aranda et al. 1984) and *A. taxiformis* (Zanolla et al. 2019), the brown seaweeds *Sargassum muticum* (Yendo) Fensholt (Thomsen et al. 2006) and *U. pinnatifida* (Schiel and Thompson 2012) and the green seaweed genus *Caulerpa*, specifically *C. taxifolia* (M. Vahl) C. Agardh (de Villèle and Verlaque 1995) and *C. cylindracea* Sonder (Ruitton et al. 2005). All these species showed the ability to maintain stable populations throughout the year, suggesting the existence of adaptive physiological mechanisms to the newly-invaded area and posing a continuous impact over native communities. Likewise, *R. okamurae* demonstrated a remarkable ability to establish dense monospecific populations, maintaining densities exceeding 3000 individuals per square metre and reaching biomass up to 170 g DW per square metre. These values greatly surpass other documented invasive seaweeds. For instance, *A. taxiformis* in the southern Iberian Peninsula, reached the highest biomass in the summer (Zanolla et al. 2017), but these values were 40% lower than those recorded for *R. okamurae* in this study. Another example was *U. pinnatifida* with a maximum density of about 100 individuals per square metre in affected areas in New Zealand (Schiel and Thompson 2012) or *S. muticum* with a maximum of 1000 individuals per square metre in Spain (Arenas and Fernández 2000). These are 97% and 67% lower than for *R. okamurae*, respectively, but this can be explained by species size differences. Density peaks of individuals were recorded in late summer and autumn, while biomass peaks were

observed in late spring and summer. This pattern suggests a seasonal variation in the species' invasiveness in *P. oceanica* meadows, with space occupation influenced either by the high influx of new recruits or the substantial biomass of larger adult individuals. A similar pattern in temporal fluctuation of invasive behaviour was observed in different invasive seaweeds, such as *S. muticum*, showing a population dynamic characterised by alternating periods dominated by either few large individuals or numerous small individuals (Arenas and Fernández 2000).

The lack of significant correlation between abiotic factors, density of individuals and biomass is useful for understanding the success and establishment of invasive species (Jehangir et al. 2024). This result suggests that *R. okamurae* can thrive under diverse physical-chemical conditions, tolerating a wide range of abiotic environmental factors, which enhances invasiveness (Alpert et al. 2000). A similar pattern was documented in *A. taxiformis*, which maintains a high productive succession of cohorts throughout the year, regardless of changing environmental conditions (Zanolla et al. 2019). During the study period, *R. okamurae* exhibited continuous recruitment, with peaks of young individuals observed in summer and autumn. Although the specific mechanisms involved were not detailed, the presence of propagules – diminute proliferous branches developed from cortical cells of the parent blade (Kajimura 1992) – was noticeable throughout the year, except in January (pers. obs.). This ability, coupled with its capacity for clonal multiplication through fragmentation (Rosas-Guerrero et al. 2020), facilitates ongoing recruitment regardless of abiotic factors. This mechanism not only adds to its continuous presence in the *P. oceanica* meadow, but also contributes to the release of new individuals into the water column. These unattached thalli can be detected at a depth of 1141 metres, where they remain photosynthetically active after light exposure (Mateo-Ramírez et al. 2023). This agrees with the propagule pressure invasion hypothesis, which emphasises the continuous input of new individuals into an invaded area (Simberloff 2009).

The identification of six successive cohorts throughout the year revealed the specific ecological strategies of *R. okamurae* for maintaining its population in the introduced area. The presence of different cohorts under varying environmental conditions suggests distinct environmental requirements for each cohort, a trait shared with other invasive species, such as *A. taxiformis* (Zanolla et al. 2019) and *U. pinnatifida* (Schiel and Thompson 2012). The population's prevalence is driven by constant recruitment and continuous generational succession. Most cohorts had a brief duration of about two months, except cohort IV, which lasted for six months. This finding suggests that the species is unable to complete the typical haplodiplontic digenetic life cycle exhibited in its native area, which usually spans more than two years and involves an annual alternation between gametophytic and sporophytic phases (Agatsuma et al. 2005). Although reproductive characterisation is still being processed, the continuous presence of propagules and monospores (pers. obs.) may indicate that the population is sustained primarily through asexual reproduction and vegetative multiplication, with sporophytes playing a key role in population maintenance. Furthermore, overlapping cohorts observed in some months allows for a continuous succession of individuals and sustained occupation of space resulting in high coverage throughout the year. This pattern, like that observed for *U. pinnatifida* in New Zealand, enhances the invasion success of the species and increases propagule pressure in invaded areas (Schiel and Thompson 2012; South et al. 2017). This continuous occupation can have more impact on the structure and function of the ecosystem than intermittent periods of

high and low coverage (Schiel and Thompson 2012) and is likely to disrupt native species and alter ecosystem dynamics, contributing to its invasive potential.

The identified cohorts might be linked to the occurrence of the species' morphotypes described in both native and introduced areas, characterised by variations in thallus thickness and width and the number of dichotomies (Sun et al. 2006; Salido and Altamirano 2020). These morphotypes appear to follow a seasonal pattern. For example, in introduced areas, the thick morphotype arises in winter and the thinner one in summer, alternating with the intermediate morphotype (Salido and Altamirano 2020). Therefore, cohort IV could align with the thicker morphotype, cohorts II and VI with the thinner morphotype and cohorts I, III and V with the intermediate morphotype. This potential association between morphotypes and cohorts provides valuable insights into the adaptability of the different morphotypes of *R. okamurae* in response to changing environmental conditions, which contributes to understanding the species' dynamics in marine ecosystems. Although this study did not explore the relationship between morphotypes and abiotic factors, identifying the environmental drivers behind morphotype development would be essential for understanding the species' invasion success and its impact on ecosystems. Theoretical frameworks exploring the connection between phenotypic plasticity and invasion success propose that invasive species could maintain high fitness across diverse environmental conditions owing to their physiological plasticity and can even thrive under unfavourable conditions (Richards et al. 2006; Gioria et al. 2023), which may explain the observed patterns in *R. okamurae*. Understanding this behaviour could deepen knowledge about the species' invasiveness and the factors influencing morphotype succession throughout the year.

Conclusion

Overall, *R. okamurae* exhibited a notable ability to persist in the *P. oceanica* meadow despite fluctuating environmental conditions. Its capacity to endure under a wide range of abiotic factors highlights its invasiveness, which is facilitated through population dynamics. This invasiveness observed in this specific habitat is further enhanced by continuous recruitment and a succession of distinct cohorts. This study also reveals temporal windows of invasiveness for *R. okamurae*, driven by an intense density of new small-sized individuals during summer and early autumn, while late spring and summer are characterised by high biomass accumulation of larger-sized individuals. These findings contribute to a deeper understanding of the invasiveness of *R. okamurae* in the *P. oceanica* meadows through population dynamics, underscoring its ability to dominate space and persist in a variety of environmental conditions. Identifying these patterns offers crucial insights into the success of *R. okamurae* and can guide effective management strategies.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: JRG, JDR, RC, MA. Data curation: JRG. Formal analysis: RC, MZ, JRG. Funding acquisition: JDR, RC, MA. Investigation: MA, RC, JRG, JDR, MZ. Methodology: JRG, MZ, JDR, MA, RC. Project administration: MA. Resources: MA. Supervision: MA. Validation: MA. Visualization: JRG. Writing – original draft: JRG. Writing – review and editing: JDR, RC, MZ, JRG, MA.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

Table A1. One-way (month) ANOVA for density (individuals x 10³ per square metre) of *R. okamurae* and biomass (g DW per square metre). Asterisks represent significant differences (P < 0.05).

	variable	df	MS	F-value	P value
One-way ANOVA	Density	6	3761825	6.49	0.002*
	Biomass	6	9291	60.61	< 0.001*

Appendix 2

Table A2. Loading factors and percentage of the variance of the two first PCA.

	PC 1	PC 2
Percentage of variance	53.2%	26.6%
Cumulative percentage	53.2%	79.8%
Variable	PC 1	PC 2
Loading factors		
T	0.51	-0.05
Max T	0.49	0.10
Min T	0.49	-0.14
S	-0.30	0.01
LH	0.41	0.05
NO ₃	-0.01	0.70
NH ₄	0.04	0.69

T, average temperature; Max T, maximum average temperature; Min T, minimum average temperature; S, salinity; LH, Photoperiod, NO₃⁻, concentration of nitrate; NH₄⁺, concentration of ammonium.

Appendix 3

Table A3. Correlation analysis between two principal components and biological variables measured (density and biomass) in the population of *R. okamurae* (n = 7).

	PC 1		PC 2	
Variable	r	P value	r	P value
Density	0.57	0.18	0.24	0.61
Biomass	0.39	0.36	0.09	0.85